

## BREEDING BIOLOGY OF THE JABIRU IN THE SOUTHERN LLANOS OF VENEZUELA

JOSÉ A. GONZÁLEZ

**ABSTRACT.**—I studied the breeding biology of the Jabiru (*Jabiru mycteria*) at Hato El Frío (state of Apure, Venezuela) during two breeding seasons. I located 22 nests during 1989–90 and 28 in 1990–91. Jabiru nests were 8–26 m from the ground in ten different species of trees, with *Sterculia apetala* the most commonly used (36.4% of the nests). Storks laid eggs between August and November. The greatest number of clutches were in September. Average clutch size was 3.4 eggs (range: 2–5;  $N = 17$ ), with four eggs the most frequent clutch size. Fledglings left their nests in January or February at the age of 12–13 weeks but were still dependent of their parents for a period of up to two months. Nest success was 47.0% in 1989–90 and 47.6% in 1990–91; productivity (fledglings/active nest) was 0.94 and 1.00 respectively. In 1990–91, only 20% of eggs produced fledglings. Most nests (75%) failed during incubation. Main causes of nest failure were abandonment, nests falling, and predation by Crested Caracaras (*Polyborus plancus*). Received 20 Aug. 1995, accepted 15 Jan. 1996.

The Jabiru (*Jabiru mycteria*) breeds east of the Andes from southern Mexico to northern Argentina (Blake 1977, Hancock et al. 1992). Despite its large size and wide distribution, the breeding biology of this stork is poorly known (Kahl 1971, Luthin 1987, Hancock et al. 1992). Kahl (1971, 1973) and Spaans (1975) reported on the status, behavior, and reproduction of the species in Argentina and Surinam. Thomas (1981) described nesting of the Jabiru in the central llanos of Venezuela (state of Guárico) and made a behavioral comparison of the species of storks that coexist in the region (Thomas 1985).

The Jabiru appears to be widespread but not abundant in the llanos of Venezuela (Ramo and Busto 1984, Ogden and Thomas 1985). I found no literature reports on the recent status of the species in this region. Conservation of the Jabiru in the llanos is threatened by continuous loss of forests and foraging sites, the massive use of pesticides in agricultural lands, and the proliferation of artificial dikes for water management (Ayazagüena et al. 1981, Luthin 1987, Morales 1990, González 1993). Luthin (1987) strongly suggested that research on the ecology and status of the Jabiru should be undertaken on each distinct population in order to develop a global conservation strategy for the species.

### STUDY AREA AND METHODS

I studied Jabirus at Hato El Frío, a 78,000-ha private cattle ranch located in the southern or flooded plains of Venezuela, between the villages of El Samán and Mantecal (7°35'–

Asociación Amigos de Doñana, Panamá 6, 41012-Sevilla, Spain.

7°55'N, 68°50'–69°00'W) in the state of Apure. The study area is a tropical wet savanna with a highly seasonal distribution of rainfall. Mean annual rainfall is 1653 mm (period: 1969–1988), with more than 80% falling between May and October (rainy season), when much of the land is flooded up to one meter. Rainfall is very scarce between November and April (dry season), when much of the land becomes dry and water is restricted to a few streams, lagoons, and deepest marshes. The climate is tropical and mean monthly temperature is more or less uniform throughout the year, ranging from 28.6°C in March to 25.4°C in July.

Following Ramia's (1967) classification of llanos landscape types, the study area belongs to the group named "savannas of banco, bajío and estero". More than 80% of the land is occupied by herbaceous savanna vegetation, while the rest is covered by gallery forests and small isolated forested islands locally called *matas*. A detailed description of vegetation communities present at Hato El Frío can be found in Castroviejo and López (1985).

The study area was surveyed daily along fixed ground routes between July and September in 1989 and 1990, for pairs of Jabirus and for nesting attempts. In 1990, a fixed-wing aircraft was also used to search for new nests. Nesting attempts were mapped. The status of every nesting attempt was then monitored weekly until the nest was abandoned by adults or until fledglings made their first flight. A mirror on an extendable pole (also used to estimate nest height) was used to observe the contents of lower nests, but in most cases it was necessary to climb the tree or to use a ladder to reach nest level. Many of the nests were inaccessible from the ground, and their status in 1989–1990 was determined by prolonged observation of the birds' behavior. During 1990–1991, a fixed-wing aircraft was used to check the contents of inaccessible nests. The sexes were distinguished by body size and length and curvature of bill (Kahl 1971), later confirmed by copulation position.

Repeated visits to wading bird nests can severely bias the reproductive parameters studied (Tremblay and Ellison 1979, Frederick and Collopy 1989b, Kushlan 1992). On each visit, the distance at which adults left the nest in response to human approach, the total time spent near each nest and the length of time it took the birds to return to the nest were recorded. Careful observations were made for possible predation attempts while in the vicinity of the nest. To minimize disturbance, nests containing chicks more than two weeks old were not climbed; after this stage, chicks were easily visible using 12× binoculars or a 20× telescope, but eight visits to nests with older chicks were made to collect regurgitation samples (González 1993). No nests were climbed more than three times during incubation and the first two weeks after hatching. In every case, I avoided stormy or rainy days and direct sunshine to prevent thermal stress to nest contents (Dusi and Dusi 1978, King 1978).

Nesting attempts were categorized as having nest construction activities and permanent occupation by a pair of Jabirus. Active nests were those in which at least one egg was laid or, in inaccessible nests, those in which continuous incubation activity by adults was observed. Successful nests were those in which at least one chick fledged, and unsuccessful nests those that lost all eggs or chicks.

## RESULTS

*Breeding dates.*—The Jabiru nesting period in the southern llanos began in the latter part of the rainy season and extended to the middle of the dry season. Laying was from mid-August to mid-November, with the greatest number of clutches laid in September (66.6% in 1989 and 50% in 1990, Fig. 1). The nesting season began later in 1989 than in 1990; in

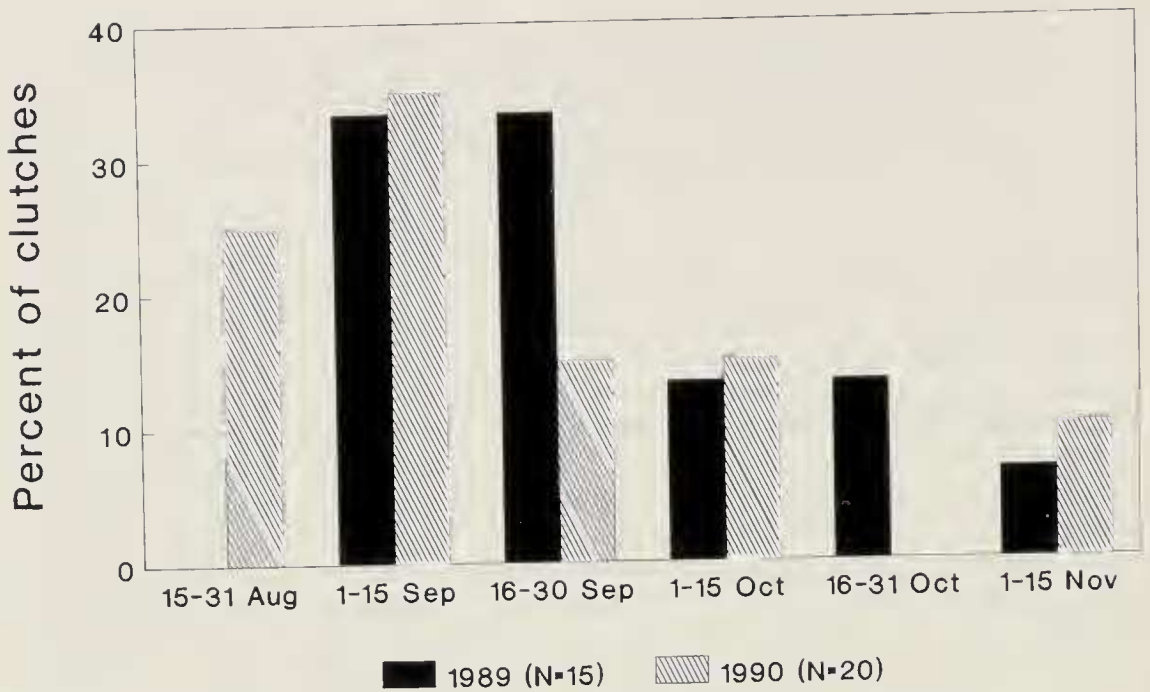


FIG. 1. Jabiru laying dates at Hato el Frío in 1989 and 1990.

the first season, no eggs were laid until September, while in 1990, 25% of the clutches were initiated in the second half of August (Fig. 1).

Nestlings stayed in the nest for about three months (84–93 days;  $N = 3$  nests). Most of the 1989 successful nestlings made their first flight from 1 to 20 January 1990 (64.3%); the remaining ones fledged in February (Fig. 2). After their first flight siblings stayed together and were fed by their parents in nearby wetlands for a period of 6–8 weeks (González 1993). Therefore, successful Jabiru pairs were involved in reproductive tasks for almost seven months a year (Fig. 2).

*Nest site.*—Most of the nests (78.1%) were in small isolated forested islands (matas) of 0.2–2 ha, 3.1% were in matas of more than 50 ha, 9.4% were in gallery forests and the remaining 9.4% were in solitary trees. Almost all the Jabiru nests were solitary and owners defended a breeding territory of 300–500 m around their nests by chasing other Jabirus and other wading bird species that flew or foraged in that area. Mean distance to nearest conspecific nest was 1.9 km (range: 1.2–2.8). Three nests were built in the center of mixed-species colonies containing other wading birds such as White-necked Herons (*Ardea cocoi*), Great Egrets (*Casmerodius albus*), and Maguari Storks (*Ciconia maguari*).

Nests generally were built at the top of one of ten different species of large broad-leaved trees. *Sterculia apetala* was the most frequently used (36.4% of the nests), followed by *Ficus* sp. (18.2%) and *Pithecellobium saman* (9.1%). Other trees that supported Jabiru nests were *Spondias*



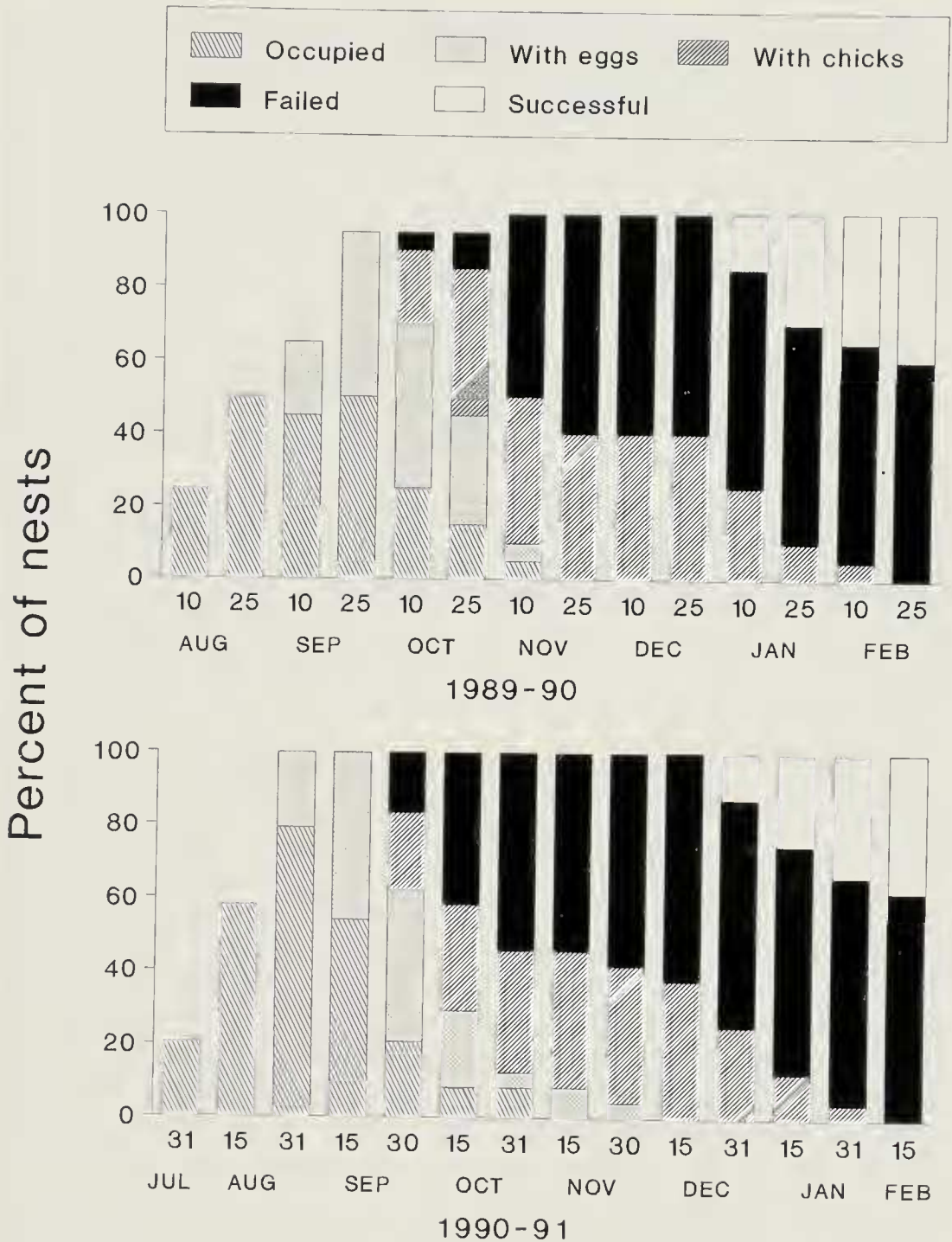


FIG. 2. Phenology of the 1989-90 (N = 20 nests) and 1990-91 (N = 24 nests) breeding seasons.

*mombin*, *Acrocomia sclerocarpa*, *Ceiba pentandra*, *Tabebuia* sp., *Sapium biglandulosum*, *Vitex* sp., and *Coccoloba caracasana*.

The average height of Jabiru nests on Hato El Frío was 15.4 m (range: 8-26). At a nearby ranch (Hato El Cedral), a nest was built less than 7

m from the ground. In nests located in dense forests (matas or gallery forests), the pair usually chose the highest tree around with an excellent view of the surrounding country. Nests were placed on forks of large limbs, between a large horizontal limb and the main trunk, or more usually in places where 3–4 branches crossed. Of the studied nests, 71.9% were on the top of the tree (crown branches), while the remaining 28.1% were on bifurcations of the trunk of a dead tree. All of the nests were less than 500 m from a large temporary or permanent wetland. Many of the nests (28.1%) were completely surrounded by deep marshes inundated during the nesting season, 21.9% were close to large permanent lagoons, and the remaining 50% were on the edge of a river or stream. These flooded wetlands were used by fledglings for 6–8 weeks after leaving the nest.

*Construction and structure of nests.*—All but two of 22 nests occupied in the 1989–1990 breeding season were reused in 1990–1991. 80% of those nests included part of their basic structure from one year to the next. The remaining 20% completely disappeared during the non-breeding season due to weather, broken supporting limbs, or the piracy of nest materials by other wading birds (in nests located in mixed-species colonies).

The time spent by *Jabirus* on nest construction before egg-laying depended on the previous state of the nest. Two nests were completely built in less than 20 days from a residual group of sticks remaining from the previous nesting season. Another nest, that kept its structure almost intact, was repaired in less than a week. The longest time it took a pair of *Jabirus* to build their new nest was seven weeks. Both sexes collaborate in nest construction or repairing, although sticks are mainly gathered by the male (Kahl 1971, Shannon 1987), at least in early stages of nest-building. In four nests monitored during an entire day, 66% of the new sticks for nest construction were gathered by the male and 34% by the female. In another nest that was apparently finished, all of the sticks and green materials were gathered by the male while the female remained on a nearby branch; only sometimes (30.7%), when the male came back with new materials, she jumped to the nest to position the sticks and then copulate. After egg-laying the female assumes a more equal role in nest-maintenance, as is the case in other storks (Kahl 1971).

*Jabiru* nests are oval to circular structures composed of sticks up to 160 cm long and 3.5 cm thick, with a central area lined with green plant material (grass, leaves and aquatic vegetation). Five nests measured during incubation averaged  $205 \times 180$  cm (range:  $180 \times 130$ – $220 \times 180$ ), with a central lined area of  $100 \times 85$  cm (range:  $80 \times 70$ – $120 \times 90$ ).

Nest thickness ranged between 40 and 60 cm, although one exceptional nest was 110 cm thick.

The gathering of sticks and green lining material continued without interruption throughout the nesting season, even in nests containing nestlings more than 80 days old and almost ready to fly. Initial size of nests changed significantly between incubation and fledgling stages. One nest was  $220 \times 170$  cm during the incubation period and reached  $270 \times 190$  cm two months later; the lined area also increased from  $120 \times 90$  to  $170 \times 130$  cm.

*Clutch size and eggs.*—Three complete clutches in 1989–1990 and 14 in 1990–1991 were counted. Grouping nests of both breeding seasons, average clutch size was 3.4 eggs (range: 2–5;  $N = 17$ ), with six nests of four eggs and five nests of two eggs. A possible replacement clutch was found. The owners of this nest lost their original clutch of two eggs in the first week of October 1990, and the same pair was seen incubating during several consecutive days in the middle of November. The nest was abandoned during the first days of December before I could corroborate the existence of a replacement clutch and its size.

The eggs of the Jabiru are ovate to subelliptical. Coloration is white but becomes dirty with the passage of time. Six eggs from three nests, measured early in incubation, averaged  $70.4 \times 53.6$  mm (length: 67.6–72.9; width: 49.8–55.9), with a mean weight of 110 g (range: 90–120).

*Nesting success.*—Of the 22 nesting attempts during the 1989–1990 breeding season, five were abandoned before egg-laying or any incubation activity by Jabirus. Three of these failed attempts were abandoned in an early stage of nest construction, while the other two nests were apparently finished and many copulations occurred in them before they were abandoned. Territorial pairs of abandoned nests remained in the area for up to two months, usually perching on the same tree that supported the nest. It is unlikely that pairs that failed during early stages of construction try to nest again in another area distant from the original one. Eight of 17 active nests during 1989–1990 fledged at least one chick (Table 1). The total number of fledglings produced in the study area was 16, with an average of 0.94 young per active nest. Nine nests (53%) failed, seven during incubation and two when they contained young chicks. Three nests fell from trees. Another had two infertile eggs that finally were abandoned. In the remaining five nests the cause of reproductive failure could not be determined. Partial losses were recorded in the eight successful nests. One egg from a clutch of three was infertile but remained in the nest for more than a week after the hatching of the other two. In two nests with initial brood size of three, the two youngest chicks were considerably smaller than their sibling and died during the first month of life,



TABLE 1

REPRODUCTIVE SUCCESS OF THE JABIRU ON HATO EL FRÍO DURING THE BREEDING SEASONS OF 1989–90 AND 1990–91

Nest variable	1989–90	1990–91
Occupied nests	22	28
Active nests <sup>a</sup>	17	21
Successful nests	8	10
% of nests successful <sup>b</sup>	47.0	47.6
Number of fledglings	16	21
Fledglings/active nest	0.94	1.00
Fledglings/successful nest	2.0	2.1

<sup>a</sup> Producing a clutch of eggs.

<sup>b</sup> Producing at least one chick to fledging age.

probably due to starvation. At another nest, one of three nestlings 65–70 days old died during a premature first flight or a fall during flapping exercises.

In the breeding season of 1990–1991 21 of 28 nesting attempts resulted in active nests. Ten were successful (47.6%). The total number of fledglings produced in the area was 21 (Table 1). Using data from 14 closely monitored nests, I estimated that only 20% of the eggs laid produced fledglings. Eight nests failed during incubation and three after hatching. One nest with two nestlings 3–4 weeks old fell when the supporting limb broke. In three failed nests, I observed Crested Caracaras (*Polyborus plancus*) eating eggs (2 nests) and nestlings 9–14 days old (1 nest); chicks and eggs were completely consumed at the nest. It is unknown whether this was predation or post-abandonment scavenging (see Frederick and Collopy 1989c). In one of these nests several days before predation, the pair of Jabirus left the eggs alone for long periods of time, which suggests that abandonment might have been the actual cause of failure. Brood reductions occurred in three successful nests, which lost a total of four nestlings. In two nests with initial brood size of three, the youngest chick died apparently of starvation; in another nest, with initial brood size of four, two chicks died during the first month of life.

#### DISCUSSION

Jabirus begin breeding in the southern llanos of Venezuela in August and some breeding occurs until February of the following year. Egg-laying takes place mainly during September, and most fledglings leave their nests in January. The dates of egg laying coincide with the period of major flooding, when adult Jabirus can easily find abundant food in

inundated marshes, mainly freshwater eels (Kushlan et al. 1985, Thomas 1985, González 1993). Fledglings make their first flight in the middle of the llanos dry season, when the absence of rains and rapid drying result in large concentrations of fishes in the few lagoons and ponds that still preserve some water (González 1993). The beginning of the breeding season, as well as nesting success of the Jabiru in the southern llanos, may be related to the onset and quantity of rainfall and the effect they have on water level and food availability. This is similar to other wading bird species that breed in wetland habitats distinguished by a marked seasonal fluctuation in water level (Ogden et al. 1980, Ayarzagüena et al. 1981, Frederick and Collopy 1989a). Breeding dates in the study area are similar to those reported in literature for *Jabirus* in other regions. Kahl (1971) reported that the egg-laying period extends from July to October in Argentina and Brasil. Spaans (1975) recorded egg laying during August and September in Surinam. Laying dates in Guyana, Brazil, and Colombia are also between July and October (in Kahl 1971). In the central llanos of Venezuela, most of the clutches are laid during September and October (Thomas 1985).

The majority of the nests found in the study area were located in forested islands (matas) of less than 2 ha, with nests most frequently placed in *Sterculia apetala*. Other Jabiru nests reported from the llanos include 11 nests in the palm *Copernicia tectorum* (Thomas 1981) and two nests in *Pithecellobium saman* (Ogden and Thomas 1985). Spaans (1975) mentioned one nest in *Ceiba pentandra* in Surinam and Kahl (1971) reported six nests in palms and other medium-size trees in Argentina. In general, *Jabirus* build nests far from other wading bird nests. However, three nests in the study area were in the center of mixed-species colonies. Naumburg (in Kahl 1971) also reported one Jabiru nest in a large colony of Wood Storks (*Mycteria americana*) in Brazil.

Average clutch size in the study area was 3.4 eggs. Most completed clutches were comprised of four eggs. Three clutches (17.6%) were comprised of five eggs, a number that is considered rare for *Jabirus* (Kahl 1971, Hancock et al. 1992). Hagmann (in Bent 1926) reported clutches of two and three eggs in Jabiru nests, while Lloyd (in Bent 1926) reported that four eggs was the most frequent clutch size in this species. Kahl (1971) reported two clutches of four eggs in Argentina. The average size of six eggs was slightly lower than average size reported by Bent (1926):  $73.4 \times 58.2$  mm ( $N = 8$ ).

*Jabirus* exhibit territoriality throughout the nesting season (Kahl 1973, Thomas 1985, Shannon 1987). As a consequence of this aggressive behavior, Thomas (1981) suggests that it is unlikely that more than one female could lay eggs in the same nest. Although I absolutely agree with



these statements, however, an exceptional event took place in one of the studied nests: for more than three hours in the morning of 3 October 1989, a male copulated repeatedly with two different females, each of which took turns in the nest; finally, one of the females was expelled by the other and left the area. The nest was abandoned three weeks after this event and no incubation activity was observed during that period.

Nest success in the study area was 47% in 1989–1990 ( $N = 17$  nests) and 47.6% in 1990–1991 ( $N = 21$  nests), with only 20% of the eggs producing fledglings ( $N = 14$  nests). There are no other published data on nesting success of this species in other geographical areas to compare with my results.

Most of the unsuccessful nests failed in an early stage of incubation. The abandonment of the nest by adults and predation upon eggs or nestlings seem to be the two most important causes of nesting failure in the studied population; it is very difficult to determine which of them occurs first (Frederick and Collopy 1989c). The Crested Caracara, an abundant raptor in the southern llanos, was the main predator of eggs and nestlings of *Jabirus* and, in general, of all wading birds in the study area (González 1993).

Of 22 nests recorded during the 1989–1990 breeding season, 19 were reused in 1990–1991 (86.4%). Thomas (1981) reported that in the central llanos of Venezuela, new nests were made every breeding season because palms supporting nests died after the first year. In the study area I found only one nest in a palm in 1989–1990; this nest fell during the incubation period and was not reused in 1990–1991.

Of the 17 active nests monitored in the first breeding season, only eight were again active during the second one. Considering the successful nests of 1989–1990 ( $N = 8$ ), only three of them were active in 1990–1991, and only two were again successful. If we assume the hypothesis that *Jabiru* pairs remain mated in successive seasons and use the same nesting site, which is supported by several observations on their nesting behavior and territoriality (Kahl 1973, Thomas 1985, González 1993), my data would indicate that less than half of active pairs in one season are also active during the following one and that only 25% of successful pairs are successful in a second consecutive season. This may be due to a mere coincidence or could suggest that *Jabirus* have some trouble breeding successfully in consecutive years, perhaps due to the great amount of time that adults spend on breeding-related activities (6–7 months). Long-term studies in the same area that include monitoring of marked birds are needed to assess these statements.

#### ACKNOWLEDGMENTS

I thank J. Castroviejo for his encouragement during this work. I also thank all the Maldonado family, owners of Hato El Frío, for their hospitality and for giving us all the facilities

to develop our work. I am grateful to F. Ibáñez, V. Rosales, P. Quiñones, and the staff of Estación Biológica El Frío for their assistance during the field work. I am also very grateful to P. Frederick, C. Ramo, E. de Juana, B. T. Thomas, and C. R. Blom for reviewing earlier drafts of the manuscript. Financial support was provided by grants of Asociación de Amigos de Doñana and Universidad Complutense de Madrid.

## LITERATURE CITED

- AYARZAGÜENA, J., J. PÉREZ, AND C. RAMO. 1981. Los garceros del Llano. Cuadernos Lagooven, Caracas, Venezuela.
- BENT, A. C. 1926. Life histories of North American marsh birds. I. U.S. National Museum Bull. 135, Washington, D.C.
- BLAKE, E. R. 1977. Manual of Neotropical Birds, Vol. 1. Univ. of Chicago Press, Chicago, Illinois.
- CASTROVIEJO, S. AND G. LOPEZ. 1985. Estudio y descripción de las comunidades vegetales del "Hato El Frío", los llanos de Venezuela. Memoria de la Sociedad de Ciencias Naturales La Salle 124:79-151.
- DUSI, J. L. AND R. T. DUSI. 1978. Survey methods used for wading bird studies in Alabama. Pp. 207-211 in Wading birds (A. Sprunt, IV, J. C. Ogden, and S. Winckler, eds.). National Audubon Society Research Report 7, New York, New York.
- FREDERICK, P. C. AND M. W. COLLOPY. 1989a. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625-634.
- AND ———. 1989b. Researcher disturbance in colonies of wading birds: effects of frequency of visits and egg-marking on reproductive parameters. Colon. Waterbirds 12: 152-157.
- AND ———. 1989c. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. Condor 91:860-867.
- GONZÁLEZ, J. A. 1993. Contribución al estudio de la ecología de las cigüeñas (Fam. Ciconiidae) en los llanos de Venezuela. Ph.D. diss., Univ. Complutense de Madrid, Madrid, Spain.
- HANCOCK, J. A., J. A. KUSHLAN, AND M. P. KAHL. 1992. Storks, ibises and spoonbills of the world. Academic Press, London, England.
- KAHL, M. P. 1971. Observations on the Jabiru and Maguari storks in Argentina, 1969. Condor 73:220-229.
- . 1973. Comparative ethology of the Ciconiidae. Part 6. The Blacknecked, Saddlebill, and Jabiru storks (Genera *Xenorhynchus*, *Ephippiorhynchus*, and *Jabiru*). Condor 75:17-27.
- KING, K. A. 1978. Colonial wading bird survey and census techniques. Pp. 155-159 in Wading birds (A. Sprunt, IV, J. C. Ogden, and S. Winckler, eds.). National Audubon Society Research Report 7, New York, New York.
- KUSHLAN, J. A. 1992. Population biology and conservation of colonial wading birds. Colon. Waterbirds 15:1-7.
- , G. MORALES, AND P. C. FROHRING. 1985. Foraging niche relations of wading birds in tropical wet savannas. Pp. 663-682 in Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds.). Ornithol. Monogr. No. 36. American Ornithologists' Union, Washington, D.C.
- LUTHIN, C. S. 1987. Status and conservation priorities for the world's stork species. Colon. Waterbirds 10:181-202.
- MORALES, G. 1990. Conservación de las aves zancudas en los llanos de Venezuela. Pp. 77-84 in The Scarlet Ibis (*Eudocimus ruber*): status, conservation and recent research (P.

- C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds.). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- OGDEN, J. C., H. W. KALE, AND S. A. NESBITT. 1980. The influence of annual variation in rainfall and water levels on nesting by Florida populations of wading birds. *Transactions of the Linnaean Society of New York* 9:115–126.
- AND B. T. THOMAS. 1985. A colonial wading bird survey in the central llanos of Venezuela. *Colon. Waterbirds* 8:23–31.
- RAMIA, M. 1967. Tipos de sabanas en los llanos de Venezuela. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 27:264–288.
- RAMO, C. AND B. BUSTO. 1984. Censo aéreo de Corocoros y otras aves acuáticas en Venezuela. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 39:65–88.
- SHANNON, P. W. 1987. The Jabiru Stork (*Jabiru mycteria*) in zoo collections in the United States. *Colon. Waterbirds* 10:242–250.
- SPAANS, A. L. 1975. The status of the Wood Stork, Jabiru, and Maguari Stork along the Surinam coast, South America. *Ardea* 63:116–130.
- THOMAS, B. T. 1981. Jabiru nest, nest building and quintuplets. *Condor* 83:84–85.
- . 1985. Coexistence and behavior differences among the three western hemisphere storks. Pp. 921–931 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds.). *Ornithol. Monogr.* No. 36. American Ornithologists' Union, Washington, D.C.
- TREMBLAY, J. AND L. N. ELLISON. 1979. Effects of human disturbance on breeding of Black-crowned Night Herons. *Auk* 96:364–369.